

AUSTRALIAN VEGETATION DURING THE TERTIARY: MACROFOSSIL EVIDENCE.

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ABSTRACT

The Australian Tertiary plant macrofossil record, although very incomplete, offers a unique insight into past vegetation composition and dynamics, and the effect of changing climate both on vegetation composition and plant evolution. During the Early Tertiary, southeastern Australia supported complex rainforests with a very high diversity of woody plant species. The prevailing climate included a moderate mean annual temperature and, more importantly, very little temperature variability away from the mean. As well as this, rainfall was high throughout the year, and humidity was also very high. There is no extant analogue either for this climate or for the vegetation it supported. As the climate cooled and temperature extremes developed, and rainfall declined and became more seasonal, rainforests in southeastern Australia declined in species numbers. Many taxa became extinct or migrated (or were restricted in range) northwards into the mid-high elevation equatorial rainforests where they, or their descendants, still occur. Some rainforest taxa evolved in response to the changing climate in southeastern Australia, although many of these were ultimately unsuccessful and became extinct in the region. As the climate further deteriorated, non-rainforest vegetation expanded in the drier and colder areas, although many of the taxa present in these expanding ecosystems may have had their origin in nutrient-poor rainforests.

KEYWORDS: Plant macrofossils, Tertiary, Australia, plant-climate interaction, vegetation reconstruction.

INTRODUCTION

The extant Australian vegetation is a complex mixture of types, which interact over large and small scales both spatially and temporally. It is generally considered that much of this complexity has a recent origin, resulting from the extremes of the rapid glacial cycles and the catastrophic effects of the arrival of Aboriginal and then European man. The magnitude of these causative factors has probably been overestimated, partly because the prevailing view has been that Tertiary vegetation in Australia was largely uniform, and varied only on very broad latitudinal and altitudinal scales. This view is still held by some palaeobotanists, but the emerging and more realistic view is that Australian vegetation has been enormously dynamic over a very long period of time, and, rather than seeing it at its most complex today, much of the landscape has suffered a substantial reduction in floristic diversity since the Early Tertiary.

Unfortunately, macrofossil evidence is still scarce, but it is accumulating rapidly, and from much farther afield than the traditional southeastern Australian coastal belt, which until recently provided almost all the data from which reconstructions of vegetation over the entire continent were based. The palynological data base is also expanding quickly, especially into central Australia. Palynological evidence provides us with the broad picture, since pollen is widely dispersed (Kemp 1978; Martin 1982; Kershaw 1988). However, this has its drawbacks when attempting to reconstruct local communities, and this is exacerbated by the current lack of taxonomic resolution in many pollen forms. The macrofossil record is much less extensive than the palynological record, but it represents local vegetation and communities and taxonomic resolution is often much greater. This allows far more detailed reconstructions of local plant communities. In this review of the available evidence the macrofossil record will be favoured for both of

these reasons, and to complement the reviews of palynological evidence already presented by several authors (e.g. Kemp 1978; Martin 1982; Kershaw 1988).

DIFFERENTIATION OF THE VEGETATION DURING THE TERTIARY

Few macrofossils of angiospermous affinity have been published from the Australian Cretaceous, and with the exception of that of Taylor and Hickey (1990) there is a lack of detailed work on these fossils. Therefore we have little real idea of the form of the vegetation prior to the Tertiary. However, it is clear that by the Early Tertiary the vegetation had differentiated, at least on a regional scale, and probably on a much finer scale as well. The oldest Tertiary macroflora known to date is in Late Paleocene sediments at Lake Bungarby in southern N.S.W. This site occurs in the eastern highlands and was deposited at an altitude of 400-800m (Taylor *et al.* 1990). The macroflora largely awaits description, but it is diverse, very large-leaved, and contains an interesting mixture of taxa. Among the angiosperms which have been identified are elements which are regarded as microthermal rainforest taxa (e.g. *Encryphia* (Hill 1991b), *Nothofagus*, and microthermal sclerophyllous taxa (*Banksiaephyllum*). There are other angiosperms which have been identified (e.g. Lauraceae), which are typical of all except the coolest rainforests, and which have such wide extant ecological tolerances that it is difficult to speculate on their palaeoecological significance. The relatively large leaf size in this deposit suggests a high mean annual temperature, but the age of this site and its high palaeolatitude means that other factors, and in particular photoperiod, may have been playing an important role in determining leaf size. This flora also contains a high diversity of small-leaved conifers, which appear to have had a significant role in cooler forests in this region during the Early Tertiary.

The plant macrofossil record of the Early Eocene is not well known, with only a few poorly described sites in southeastern Australia yielding data to date. This includes sites in Tasmania which are notable for their high conifer diversity (Townrow 1965a, 1965b; Bigwood and Hill 1985; Hill and Bigwood 1987; Hill and Carpenter 1991) and the predominance of small to medium sized angiosperm leaves, at least some of which have microthermal living relatives (e.g.

Encryphia (Hill 1991b)). The Early Eocene Deane's Marsh locality in Victoria is of particular interest. The only macrofossil described from this site is a *Banksiaephyllum* species (Hill and Christophel 1988), but Christophel and Greenwood (1989) consider that the leaf size of the fossils most closely allies the vegetation with microphyll mossy forest, thus making this site particularly cool for the time. Unfortunately, they did not publish any of the data associated with this conclusion, so the details are uncertain.

Middle Eocene macrofloras on the coastal margin of southeastern Australia are notable for their extraordinary complexity (Christophel and Blackburn 1978; Christophel *et al.* 1987; Christophel and Greenwood 1987), but it is interesting that conifers are relatively scarce, and their diversity is low in comparison to both earlier and later macrofloras (Table 1). No microthermal elements have been described from these floras, although taxonomically they are very poorly understood. The Early-Middle Eocene boundary Nerriga macroflora occurs further inland and at a higher elevation and has a lower diversity, with clear dominants present (Hill 1982, 1986, 1989). However, there is no evidence for microthermal taxa in this deposit either.

Middle-Late Eocene macrofloras from Vegetable Creek (northern NSW) and Tasmania once again have a microthermal angiosperm element (e.g. *Nothofagus* (Hill 1988), *Encryphia* (Hill 1991b)) and a prominent and diverse conifer element (Ettingshausen 1888; Hill and Carpenter 1991). Because of their geographical separation it is not yet clear whether the coastal Middle Eocene floras (Anglesea, Maslin Bay, Golden Grove) represent a genuine shift in vegetation at that time away from microthermal taxa, or whether they reflect a coastal vegetation type which persisted for a much longer time both before and after the Middle Eocene.

Oligocene rainforests are only known from Tasmania, where several deposits demonstrate a shift towards even more microthermal vegetation, with a reduction in the number of taxa which have their extant relatives at low latitudes. There can be little doubt that this floristic shift is a direct response to climatic change, most probably a slight decrease in mean annual temperature coupled with the development of a more seasonal climate, with the consequent onset of frost as an important environmental determinant. However, even during the Tasmanian Oligocene there is a mixture of species in single

vegetation types which now occur over a very wide latitudinal range (about 40°). This is interpreted as being due to the presence of a climate which was more equable than any now occurring in the region (Hill 1990b). Mainland Oligocene vegetation is represented by the Latrobe Valley coal (Duigan 1966; Blackburn 1985) and possibly a site at Westdale in Western Australia (Hill and Merrifield in press). Both sites have a distinctive sclerophyllous element, which may be representative of a general shift towards a more xeric climate on mainland Australia. Although the data are too sparse to emphatically support this as a general conclusion, it is clear from palynological evidence that such environments were expanding at this time.

Miocene macrofloras are rare in Australia and are, in general, poorly studied. The Latrobe Valley coal is an exception, and again provides strong evidence of at least localised sclerophyllous (nutrient-poor) and occasional xeric conditions (Blackburn 1985). Other macrofloras are suggestive of microthermal *Nothofagus*-dominated rainforest in southeastern and eastern Australia (Bacchus Marsh (Christophel 1985), Vegetable Creek (Eutinghausen 1888; Hill unpublished data), and in Tasmania there is evidence for the presence of complex subalpine woodland at high altitude by the onset of the Miocene (Hill and Gibson 1986; Macphail *et al.* 1991).

Pliocene macrofloras are unknown in Australia, but an Early Pleistocene macroflora on the west coast of Tasmania is providing abundant evidence for the importance of the Quaternary glacial cycles as agents of ecological silting (Hill and Macphail 1985, in press; Jordan and Hill 1991). Many taxa have been recovered from

these sediments which are now extinct in Tasmania and which have their nearest living relatives on mainland Australia, sometimes far removed from Tasmania (G.J. Jordan pers. comm.). This suggests that at least some of the complexity present in Eocene-Oligocene rainforests in the region was still present in the Pleistocene and was progressively reduced with succeeding glacial cycles.

Thus the general picture which emerges of Tertiary rainforest in southeastern Australia is of a very complex mosaic in the Early Tertiary, containing microthermal and mesothermal lineages. This rainforest has no modern analogue and is presumed to have developed under an extremely equable climate which similarly has no modern analogue. The mean annual temperature was probably higher than at present, but not excessively so. The important feature of temperature was more likely to have been a lack of extremes and certainly frost is unlikely to have been an important environmental factor. Part of the reason for the lack of temperature extremes was probably the high year round rainfall and humidity. Nix (1982) provides a very good summary of the important factors of Tertiary climates from the perspective of plant growth, and predicts climatic zones for the Tertiary right across Australia. Later in the Tertiary, when temperature declined and became more variable, and rainfall declined and became more seasonal, the Early Tertiary rainforest elements separated. Some appear to have "followed" the most suitable climate, and now occur at moderate to high altitudes in New Guinea. Others remained in the region and in many cases evolved substantially in response to the changing climate. Some examples of these taxa are consid-

Table 1. Species numbers in selected genera and families (in brackets) which are prominent in Tasmanian fossil deposits. The Tasmanian sites are Regatta Point (Early Eocene), Cethana (Early Oligocene), Pioneer and Little Rapid River (Oligocene) and Monpeelyata (Late Oligocene-earliest Miocene). Three Eocene sites from southeastern mainland Australia (Maslin Bay, Anglesea and Nerriga) are shown for comparison. Data from Blackburn (1981), Carpenter (1991), Christophel *et al.* (1987), Greenwood (1987), Hill (1990b, 1991), Hill and Bigwood (1987), Hill and Carpenter (1991), Hill and Christophel (1988), Wells and Hill (1989).

Site (estimated total species diversity in brackets)	<i>Banksiaephyllum</i> <i>Banksiaeformis</i> (Proteaceae)	<i>Nothofagus</i> (Fagaceae)	<i>Araucaria</i> (Araucariaceae)	<i>Dacrycarpus</i> (Podocarpaceae)
Regatta Point (> 40)	1 (2)	0	≥ 4 (6)	2 (6)
Cethana (> 100)	7 (≥ 18)	≥ 5 (5)	≥ 2 (5)	1 (≥ 12)
Pioneer (> 25)	1 (2)	1 (1)	0 (1)	2 (6)
Little Rapid River (> 40)	0 (2)	≥ 4 (4)	1 (2)	5 (13)
Monpeelyata (> 20)	0 (1)	2 (2)	3 (3)	3 (5)
Maslin Bay (> 200)	2 (3)	0	0 (1)	0 (1)
Anglesea (> 80)	1 (5)	0	0	1? (6)
Nerriga (> 25)	0 (1)	0	0	0 (1)

ered in the next section. Some taxa migrated northwards, but also remained in the region, evolving substantially in response to climate change. However, in most of these cases, they appear to have been ultimately unsuccessful, probably disappearing from southeastern Australia during the Late Tertiary or during the Quaternary glaciations.

One of the particularly interesting features of Tertiary vegetation in southeastern Australia is that not only is the species diversity usually very high, but the diversity within particular genera is also often high. Examples of this include the angiosperm genera *Nothofagus* and *Banksiaephyllum* (*Banksia/Dryandra*) and the conifer genera *Dacrycarpus* and *Araucaria* (Table 1). This is particularly interesting, since it is rare to see such a diversity within single genera in a single catchment area today, even when the regional diversity of a genus is high (e.g. *Banksia* in southwestern Australia or *Araucaria* in New Caledonia). The reason(s) behind this high diversity of species within single genera are uncertain, but there is no doubt that it was highly significant for animal species which depended upon them as food sources or for other aspects of their ecological niche.

PLANT EVOLUTION IN RESPONSE TO CLIMATE CHANGE

Many of the changes in diversity described above are simply a result of changes in species' distributions in response to climate change. However, there is abundant evidence for plant evolution during the same time period, and most of it can be closely related to climatic change. Within rainforest vegetation in Tasmania there is clear evidence for evolution of leaf form in response to changes in both temperature and rainfall. Leaves are the most common plant macrofossils, and as the physiological work-houses of the plant they are also the most sensitive to climate change. In the past this has often led to the conclusion that leaves are unreliable taxonomic units, since they are so morphologically responsive to local microclimate, but it is now becoming clear that this responsiveness is a very useful tool for the analysis of past climates.

The most obvious change in leaf morphology in southeastern Australia during the course of the Tertiary is a reduction in leaf size. Paleocene-Eocene rainforests generally had large leaf sizes (Fig. 1), and although this may be partly a result

of the unusual photoperiod at very high latitudes, there is no doubt that the over-riding factor controlling this was temperature. It has been known for a long time that large leaf size is correlated with a high mean annual temperature and that leaf size generally declines with increasing latitude as long as rainfall is not limiting. It is also clear that the living relatives of many of the Eocene species now occur in meso-megathermal forests at low latitudes, which is in accord with this conclusion. In many cases the transition from large- to small-leaved plants during the Tertiary in southeastern Australia is the result of species replacement, but in some cases there are clear phylogenetic lines involved.

The best documented example is within the *Nothofagus moorei*-*N. cunninghamii* complex. *Nothofagus moorei* is a large-leaved, evergreen species which occurs today in small pockets of high altitude rainforest in northern New South Wales and southern Queensland, while *N.*

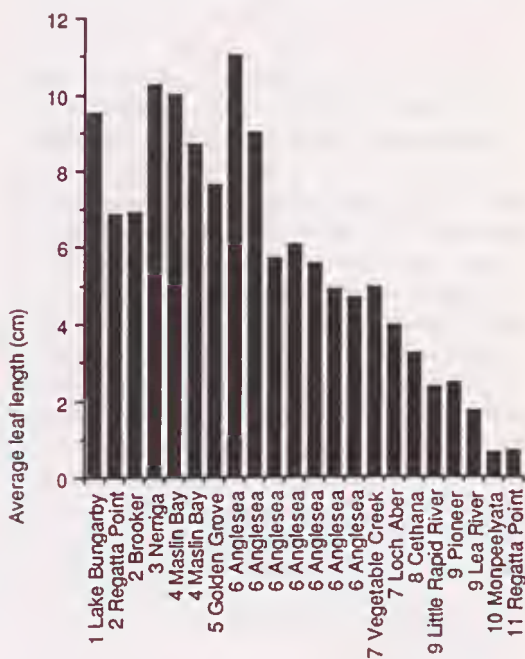


Fig. 1. Histogram showing average length of angiosperm leaves from Tertiary sediments in southeastern Australia. Note the general trend towards decreased leaf size in more recent sediments. The ages of the sites shown are: 1 = Late Paleocene; 2 = Early Eocene; 3 = Early-Middle Eocene boundary; 4 = early Middle Eocene; 5 = Middle Eocene; 6 = late Middle Eocene; 7 = Late Eocene; 8 = Early Oligocene; 9 = Oligocene; 10 = Late Oligocene-earliest Mioocene; 11 = Early-Middle Pleistocene. Data derived from Christophel and Blackburn (1978), Christophel (1981), Christophel and Greenwood (1987, 1988, 1989), D.R. Greenwood (pers. comm.) and Hill, Carpenter and Jordan (unpublished data).

cunninghamii is a small-leaved evergreen rainforest dominant in Tasmania and parts of Victoria (Table 2). Paleocene and Eocene leaves from southeastern Australia which are related to these extant species all closely resemble *N. moorei* in leaf size and morphology (Hill 1988, 1991a). However, during the course of the Tertiary in Tasmania this lineage decreased in leaf size and changed in morphology until by the close of the Tertiary it is recognisable as *N. cunninghamii* (Hill 1983, 1991a). During this time period in New South Wales, more limited evidence suggests that the fossils more or less retained their original form, resulting in the extant *N. moorei*. Thus the Tasmanian lineage has evolved considerably in leaf size and morphology, presumably in response to the decrease in mean annual temperature which took place in Tasmania during the Tertiary. Although the fossil evidence for other taxa is limited, there is compelling evidence from the leaf size of closely related species in temperate rainforests of New South Wales and Tasmania to suggest that this leaf size reduction was a general phenomenon (Table 2).

There is also evidence to suggest that evolution in leaf form took place in response to changing rainfall patterns. This evidence is best documented in the conifer family Podocarpaceae, but is supported by evidence from angiosperm leaves as well. The podocarp genus *Acmopyle* is very restricted today, with one species in New

Caledonia and the other known from only six collections in Fiji. However, it is known as a macrofossil from several Early Tertiary sites in southeastern Australia and demonstrates an elegant pattern of evolution in response to declining water availability.

The oldest *Acmopyle* macrofossils (Late Paleocene) are fully amphistomatic, i.e. they have stomates equally distributed over both leaf surfaces. This suggests that water was plentiful throughout the year for this species and that water loss was never a serious problem (Hill and Carpenter 1991). Therefore the plant has maximised its stomatal distribution in an attempt to maximise photosynthesis and growth. By the Early Eocene *Acmopyle* had begun to lose stomates on one leaf surface, suggesting that control of water loss was developing as a serious problem, and the species had adapted morphologically by reducing its stomatal distribution, presumably with the consequence that net photosynthesis was also reduced (Hill and Carpenter 1991). That is, the plant was adapting to a harsher environment, but at a cost in terms of potential growth. This trend continued throughout the Eocene, and by the Late Eocene one species of *Acmopyle* had evolved to the point where stomates were reduced to one leaf surface. The last record of *Acmopyle* in southeastern Australia is from the Early Oligocene, and it can be assumed that at about this time the climate changed to such a degree that *Acmopyle* was no longer able to evolve a competitive response to it and thus became extinct in the region. It is interesting that the two living species of *Acmopyle* both have a stomatal distribution similar to that of the Early Eocene species in Tasmania: there are stomates on both leaf surfaces, but they are relatively restricted on one of them. This suggests that the prevailing climate over the range of living *Acmopyle* is suboptimal, but that it is not as severe as the genus can withstand.

The podocarp genus *Dacrycarpus* illustrates an interesting combination of response to both temperature and rainfall changes. *Dacrycarpus* has two foliage types. In one type the leaves are bilaterally flattened, so that each functional leaf surface is composed of both adaxial and abaxial leaf surfaces. Furthermore, the whole short shoot (a single season's growth) is flattened into two dimensions, so that the short shoot probably functions like a single broad angiosperm leaf. As well as this, *Dacrycarpus* produces small, scale-like bifacially flattened leaves, which are arranged spirally around the axis in an imbricate

Table 2. Mean leaf area (mm²) of species in common genera from temperate rainforest in Tasmania or northern New South Wales (standard deviation in brackets). *Nothofagus cunninghamii* is separated into Victorian and Tasmanian populations. In each case, the species from lower latitudes has a significantly higher leaf area. Glasshouse experiments demonstrated that a large part of this difference in leaf area is genetically fixed. Adapted from Hill and Read (1987).

Species	(location)	Leaf area	(standard deviation)
<i>Acradenia euodiiformis</i>	(N.S.W.)	9817	(3424)
<i>A. frankliniae</i>	(Tas.)	756	(338)
<i>Anopterus macleayanus</i>	(N.S.W.)	13846	(3326)
<i>A. glandulosus</i>	(Tas.)	3420	(1664)
<i>Eucryphia moorei</i>	(N.S.W.)	2278	(1024)
<i>E. lucida</i>	(Tas.)	405	(140)
<i>E. milliganii</i>	(Tas.)	75	(33)
<i>Nothofagus moorei</i>	(N.S.W.)	1649	(692)
<i>N. cunninghamii</i>	(Vic.)	130	(59)
<i>N. cunninghamii</i>	(Tas.)	83	(36)
<i>Trochocarpa laurina</i>	(N.S.W.)	566	(310)
<i>T. disticha</i>	(Tas.)	62	(20)
<i>T. gunnii</i>	(Tas.)	31	(10)
<i>T. cunninghamii</i>	(Tas.)	24	(12)

arrangement. In most living species these two foliage forms appear at random on the plant, although the bilaterally flattened foliage is often considered to represent juvenile foliage.

Dacrycarpus macrofossils are particularly abundant in Early Tertiary sediments in Tasmania (Wells and Hill 1989; Hill and Carpenter 1991), and demonstrate a clear trend in foliage evolution. In Early Eocene sediments, both foliage types are very common, and stomates occur all over both leaf surfaces. However, in progressively more recent sediments there is a trend in two aspects of leaf morphology. Firstly, the bilaterally flattened foliage becomes less common, and by the end of the Oligocene is no longer present as a macrofossil. Secondly, in the bifacially flattened foliage stomates become progressively more restricted to the inner (adaxial) leaf surface, and by the end of the Oligocene are only found in that position. No *Dacrycarpus* macrofossils have been found in Tasmania after the earliest Miocene, but pollen is recorded up until the Early-Middle Pleistocene (Hill and Maephail 1985, in press), suggesting that *Dacrycarpus* may have been a victim of the Quaternary glacial cycles. Thus in this genus we see the reduction in leaf area noted earlier for *Nothofagus*, and presumably a response to declining mean annual temperature, as well as a restriction in the distribution of stomates, which is interpreted as a response to the onset of seasonal rainfall and possibly a decrease in total annual rainfall as well. The other interesting feature of *Dacrycarpus* is that these trends are seen in more than one phylogenetic line, suggesting that these were general convergent trends in foliage in response to common external factors (Hill and Carpenter 1991).

There is also some evidence for evolution or possibly species replacement in response to far more pronounced changes in water availability during the Tertiary. In Early Tertiary rainforest floras there is often an element present which, in terms of its taxonomic affinity and its leaf structure, is best considered as sclerophyllous. This group is most prominently represented by the Casuarinaceae and Proteaceae (particularly the genus *Banksiaeaephyllum*). Sclerophylly is presumed to be a primary response to low soil nutrient levels (e.g. Loveless 1961), although it is also frequently observed as a xeromorphic response. In the Early Tertiary representatives it is probable that low nutrient levels were the only factors acting, since it has already been noted

that water was plentiful in these sites, and in all fossil leaves examined there are no morphological adaptations to protect the stomates. Such adaptations would be expected if lack of water was an important factor. However, there is no doubt that some of the sclerophyllous characteristics of these plants (thick cuticles, small leaves, large proportion of water conducting tissue etc.) preadapted these plants to decreased water availability when lower and more seasonal rainfall developed later in the Tertiary (Hill 1990a). Therefore these plants would have been able to exploit marginal rainforest habitats and probably quickly evolved more xeromorphic adaptations to exploit the developing arid regions. Thus in the later Tertiary we see similar leaves to those sclerophylls which were present in the Early Tertiary, but they have developed more obvious stomatal protection mechanisms.

While the Tertiary evolution of xeromorphic characters seems to be a viable hypothesis, it is equally if not more likely that what we see in the fossil record is not evolution in response to developing aridity, but radiation of a previously restricted flora. It is probable that during the Early Tertiary there were dry microsites (e.g. sand dunes, ridgetops) which would have been populated by a highly xeromorphic flora, possibly closely related to the less xeromorphic sclerophylls which were present in and around rainforest. These xeromorphs were in sites where fossilisation was highly unlikely, and coupled with their restricted distribution this means that they have not left a detectable macrofossil record to date. As the climate dried these xeromorphic plants radiated rapidly, and supplanted rainforest in many areas, in the process appearing for the first time in the macrofossil record. Thus these plants did not evolve xeromorphic adaptations during the onset of widespread aridity during the Late Tertiary, but simply expanded their range. It is probable that macrofloras away from the coastal southeastern Australian region hold the best hope of determining between these two hypotheses.

The role of xeromorphic preadaptation may also have been important in the early development of the Australian alpine flora. The best macrofossil example of this is at Monpeclyata, at about 900m ASL in central Tasmania. The Late Oligocene-earliest Miocene lake sediments contain abundant plant macrofossils (Hill and Gibson 1986; Hill 1990a; Maephail *et al.* 1991), many of which are extremely small sclerophyllous leaves,

reminiscent of the present Tasmanian alpine flora. The presence of a small log at Monpeelyata demonstrates that it was below the tree-line, but there is no doubt that many of the plants present would have been well suited to treeless vegetation at high altitude when the appropriate conditions developed. It is probable that the species involved had a similar origin to the xeromorphic sclerophylls described earlier, since many of the sclerophyllous responses would preadapt a plant to cold as well as dry conditions.

One interesting feature of the macrofossil record of scleromorphic plants in Australia is the apparent scarcity of *Eucalyptus*. Although a Tertiary macrofossil record for this genus is now well established (Lange 1978; Holmes *et al.* 1983), it appears to have been a relatively minor component of most Tertiary ecosystems, especially in comparison with its abundance under a wide diversity of conditions today. There is compelling evidence to suggest that increasing fire frequency within the relatively recent past (<200,000 years) has been a major factor in the rise to dominance of *Eucalyptus* (Singh *et al.* 1981), and there is certainly evidence to suggest that an absence of fire sees the removal of *Eucalyptus* from at least some ecosystems (Withers 1978). The source of this increased fire frequency is uncertain, but the options appear to be climatic change or the introduction of fire by Aborigines as part of their food gathering regime. However, it would be unwise to discount the significance of rapidly changing climates during the glacial cycles as an agent for the rapid increase in *Eucalyptus* biomass in Australia, and possibly also a rapid increase in species numbers as new habitats were exploited. Whatever the explanation, it is clear that the current dominance of the Australian landscape by eucalypt communities is a recent event, which masks much of the underlying long term evolution which formed the basis of the Australian vegetation.

CONCLUSION

Although the Tertiary plant macrofossil record is incomplete, there is strong evidence for several general conclusions. During the Early Tertiary, southeastern Australia supported complex rainforests with a very high diversity of woody plant species present. These forests undoubtedly occurred under very equable conditions, with a

moderate mean annual temperature and, more importantly, very little temperature variability away from the mean. As well as this, rainfall was high throughout the year, and humidity was also very high. There is no extant analogue of this climate and hence no living vegetation which can be regarded as particularly similar to these forests, at least floristically and probably also structurally. There was altitudinal and latitudinal zonation of vegetation, and probably a reasonable degree of regionalisation of vegetation under similar climatic zones. High latitude and/or high altitude sites had a microthermal element prominent, with *Nothofagus* usually present, and often dominating the macroflora. This feature extended to moderate latitudes in Tasmania following the cooling event during the Late Eocene. Another interesting feature of these cooler climate floras is the high generic and specific diversity and number of specimens of conifers, both in comparison with lowland coastal Middle Eocene sites and also most rainforests in Australia today. At their peak in Oligocene sites in Tasmania and high latitude Eocene sites, conifers had a diversity which is unmatched in any vegetation type worldwide today, and probably was rarely, if ever surpassed in any vegetation in the past. A further point of interest is that the high species diversity in these floras often included large numbers of species from single genera, a phenomenon which has not been adequately explained and which is rarely seen today.

As the climate cooled and temperature extremes developed, and rainfall declined and became more seasonal, rainforests declined in species numbers as many taxa became extinct or migrated (or were restricted in range) northwards into the mid-high elevation equatorial rainforests where they, or their descendants, still occur. Many rainforest taxa evolved in response to the changing climate in southeastern Australia, although many of these were ultimately unsuccessful and became extinct in the region. As the climate further deteriorated, non-rainforest vegetation expanded in the drier and colder areas, although many of the taxa present in these expanding ecosystems may have had their origin in nutrient poor rainforests. It is probable that during the Early Tertiary, before the development of widespread arid and semi-arid conditions, much of central Australia was covered with a peculiar form of sclerophyllous and/or "xeromorphic" rainforest, which probably has no modern analogue. The history of this vegeta-

tion is largely unknown, although some evidence for it exists (Lange 1978; Hill and Merrifield in press).

Much more evidence is required before the macrofossil record can supply detailed regional vegetation reconstructions. However, there is no doubt that the evidence available at present has allowed the generation and testing of important hypotheses concerning the origin and evolution of some of the important vegetation types which could not have obtained in any other way.

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